

RESEARCH

Survival of *Coelaenomenodera lameensis* (Coleoptera: Chrysomelidae) in Relation to the Physical Characteristics of Different Oil Palm (*Elaeis* sp.) Breeding Populations

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ABSTRACT. The edibility of different *Elaeis* sp. breeding populations present in Benin was tested for the leaf miner *Coelaenomenodera lameensis* Berti (Coleoptera: Chrysomelidae), a major oil palm pest in Africa. Experiments carried out in sleeves revealed the oviposition capacities of females and the mortality rates for the different developmental stages by comparing the populations found on two breeding populations of *Elaeis oleifera* (HBK) Cortes, four of *Elaeis guineensis* Jacquin and four (*E. guineensis* × *E. oleifera*) × *E. guineensis* backcrosses. Females laid their eggs similarly on all breeding populations, with a preference for the *E. guineensis* La Mé origin. The average hatching rate reached 80% for the La Mé origin as opposed to 28% for the Deli origin. The mortality rates for the larval instars were greater on *E. oleifera*, on certain backcrosses and on the Deli origin of *E. guineensis*. Development at the second- and third- larval instars was the most affected, with a mortality rate of three to five times greater than that seen on La Mé. Epidermis and cuticle measurements indicated which breeding populations were suitable or unsuitable for the development of *C. lameensis*. *E. guineensis*, with its thin epidermis (12 µm) and cuticle (2 µm), proved to be highly susceptible to *C. lameensis* attacks. On the other hand, *E. oleifera*, which is very resistant, exhibited a thicker epidermis (17 µm) and cuticle (4 µm). The breeding populations were thus classified according to the positive or negative influence they exerted on the insect's egg laying and feeding.

RÉSUMÉ. La comestibilité de différents matériels végétaux d'*Elaeis* sp. présents au Bénin est testée pour *Coelaenomenodera lameensis* Berti (Coleoptera: Chrysomelidae), important ravageur du palmier à huile en Afrique. Des expérimentations en manchons ont permis de déterminer les capacités d'oviposition des femelles et les taux de mortalité des différents stades de développement (œufs, larves, nymphes et adultes) en comparant les populations observées sur deux origines d'*Elaeis oleifera* (HBK) Cortes, quatre origines d'*Elaeis guineensis* Jacquin et quatre Backcross (*E. guineensis* × *E. oleifera*) × *E. guineensis*. Les femelles pondent indifféremment sur tous les types de matériel végétal avec une préférence pour l'origine La Mé d'*E. guineensis*. Le taux moyen d'éclosion atteint 80% pour l'origine La Mé contre 28% pour l'origine Deli. Le taux de mortalité des stades larvaires est plus important sur *E. oleifera*, sur certains Backcross et sur l'origine Deli d'*E. guineensis*. Le développement des deuxième et troisième stades larvaires sont les plus affectés avec un taux de mortalité 3 à 5 fois supérieur à celui observé sur La Mé. Des mesures d'épiderme et de cuticule mettent en évidence l'existence de matériel végétal favorable ou défavorable au développement de *C. lameensis*. *E. guineensis* dont l'épiderme (12 µm) et la cuticule (2 µm) sont peu épais se révèle être très sensible aux attaques de *C. lameensis*. Au contraire, *E. oleifera* présente un épiderme (17 µm) et une cuticule (4 µm) plus épais et est très résistants. Le matériel végétal est ainsi classé suivant l'influence positive ou négative qu'ils exercent sur la ponte et l'alimentation des insectes.

Key Words: *Coelaenomenodera lameensis*, comestibility, oil palm, population dynamics, breeding population

The oil palm is a monocot of the family Arecaceae and of the tribe Coccoineae belonging to the genus *Elaeis*. The genus contains three species: *Elaeis guineensis* Jacquin originating from Africa, *Elaeis oleifera* (HBK) Cortes originating from South America, and *Elaeis madagascariensis* Beccari found in Madagascar. The most widespread species, *E. guineensis*, is grown for its fleshy fruits, from which mesocarp palm oil is extracted, and its kernel, from which palm kernel oil is extracted. *E. oleifera* is richer in unsaturated fatty acids. It displays some very worthwhile characteristics for genetic improvement, notably slow vertical growth, the quality of its oil, and resistance to several fungal diseases.

In oil palm breeding programs, *E. guineensis* and *E. oleifera* palms selected in several geographic origins are inbred or crossed to make breeding populations of restricted origin, intra- or inter-specific hybrids, and backcrosses (Corley and Tinker 2003). Backcrosses involve crosses between a parent of purely *E. guineensis* origin and a parent arising from a hybridization between the two species of interest (*E. guineensis* × *E. oleifera*). They are used to introgress traits

of interest from *E. oleifera* (Eo) into the genome of *E. guineensis* (Eg) (Le Guen et al. 1991). In our study, we focused on BC1 backcrosses ((Eo × Eg) × Eg).

Elaeis sp. is a target for many insect pests. The leaf miner *Coelaenomenodera lameensis* Berti and Mariau (Coleoptera: Chrysomelidae - Cassidinae) is considered to be the most harmful hispine pest in West Africa (Jacquemard 1995). This insect is linked to the oil palm and is endemic in the wettest zone of the Guinean forest where oil palms grow in their natural state (Cachan 1957a).

Among the many hispines that are widespread throughout the tropical belt, the genus *Coelaenomenodera* has 38 species, including *Coelaenomenodera elaeidis* Maulik and *C. lameensis* Berti and Mariau (synonyms: *C. elaeidis* Maulik at the outset, then *Coelaenomenodera minuta* Uhmman until determination by Berti and Mariau [1999]). Insects develop, feed, and spend virtually their entire life cycle inside galleries mined on the underside of oil palm fronds. The total duration of the cycle is estimated at 90–100 d (Cotterell 1925). Larvae hatch in 20 d, on average. The four larval stadia are spread over 40–44 d (L1,

11 d; L2, 9 d; L3, 9 d; and L4, 15 d, [Cachan 1957a](#)). The pupal stadium lasts from 15 to 22 d, and the imago remains in the gallery for 1–2 d. Adults leave the gallery for mating 3–4 d after emergence ([Cachan 1957a](#)). They can survive for 17 d on the underside of leaflets prior to oviposition ([Morin and Mariau 1971](#), [Mariau and Besombes 1972](#)). The female deposits its eggs at the bottom of a furrow that is parallel to the midrib. The furrows reach 12–15 mm in length. They are excavated over the entire thickness of the leaflet from the lower epidermis to the upper epidermis, which dries out at that spot. Fecundity varies greatly, depending on climatic factors ([Mariau and Lecoustre 2000](#)). It also varies depending on the time of year and can range from a few dozen to several hundred eggs per female ([Morin and Mariau 1971](#), [Mariau et al. 1981](#)). The eggs are partially encased in a yellow shell and covered with a fibrous agglomerate. Incubation lasts 28 d ([Cachan 1957a](#)).

The natural range of *Coelaenomenodera* spp. covers central and western Africa (Benin, Cameroon, Ivory Coast ([Patterson 1918](#), [Maulik 1920](#), [Cotterell 1925](#), [Jover 1950](#)), Ghana ([Anonymous 1910](#)), Nigeria, and Sierra Leone ([Hargreaves 1937](#)).

During outbreaks, *C. lameensis* causes severe defoliation, leading to approximately 50% production losses in the following 2 yr ([Mariau and Besombes 1972](#); [Philippe 1990, 2003](#)).

The most harmful damage is inflicted by larvae, which, at a rate of four to six galleries per leaflet, cause whole fronds to dry out, beginning with the lower fronds in the leaf crown ([Berti and Mariau 1999](#)). Generalized desiccation results from the growth and merging of galleries mined by the larvae.

In 2002, the plantations at the Pobè research center in Benin were subjected to strong pressure from a *C. lameensis* outbreak that resulted in severe defoliation of the oil palms ([Coffi 2003](#), [Philippe 2003](#)). It is known that *Coelaenomenodera* outbreaks can occur under favorable biotic and abiotic conditions ([Morin and Mariau 1974](#); [Mariau and Morin 1972, 1974](#)).

Some preliminary observations in the field showed that the distribution of this pest's populations, based on the type of defoliation, matched that of the oil palm origins ([Philippe 2003](#)). *E. oleifera* seemed less affected than *E. guineensis* ([Philippe 1977](#), [Coffi 2006](#)). Some differences in susceptibility were also seen within the *E. guineensis* ([Coffi 2006](#)). [Coffi \(2006\)](#) also showed that mortality rates for the larval instars were more pronounced in backcrosses than in individuals of the *E. guineensis* species.

For breeders, entomological analyses are a preliminary stage in the process of testing for the existence of genetic variability within the genus *Elaeis* for susceptibility to *Coelaenomenodera*, involving comparisons of the nutritional qualities, from the insect's point of view, of two species, *E. guineensis* and *E. oleifera*.

The aim of this study was to take into account the genetic characteristics of different breeding populations of the genus *Elaeis* in the feeding preferences of *C. lameensis*. Such genetic variability may be responsible for some major variations in foliage quality ([Edmunds and Alstrad 1981](#), [Perry and Pitman 1983](#)). The effect of this genetic variability of oil palm on *C. lameensis* is of great interest for selecting palms displaying resistance or low vulnerability ([Coffi 2006](#)).

Under natural conditions of the Pobè station in Benin, [Coffi et al. \(2013\)](#) showed that differences in susceptibility between origins existed within *E. guineensis*, with *C. lameensis* preferring to lay its eggs on the Yocoboué origin (Ivory Coast), which offers the best conditions for the insect's development. The susceptibility of *E. guineensis* oil palm clones was recently studied in Ivory Coast without being associated with any particular parameters ([Konan et al. 2014](#)). Among the hypotheses proposed to explain the differences in susceptibility between different breeding populations, [Coffi et al. \(2012\)](#) showed the toxicity for insects of secondary phenolic compounds extracted from the leaflets of *E. oleifera*.

We tested the hypothesis that the differences in susceptibility discovered by [Coffi et al. \(2013\)](#) could also be linked to the physical characteristics of leaflets. This hypothesis was suggested in 2006 by Philippe.

To that end, we studied the ability of the insect to lay eggs on the foliage under controlled conditions and the possibilities for the larvae to develop on different breeding populations using tests in cages, which were sleeves installed on the palms. At the same time, the physical characteristics of the leaflets likely to be linked to the conditions required for insect development were studied on the same breeding populations.

The results were analyzed with the aim of demonstrating the importance of oviposition preference and the edibility of the different breeding populations for *C. lameensis*, with the purpose of identifying sources of oil palm resistance to this pest.

Materials and Methods

Field Site, Biological Material, and Observations. Observations were carried out under natural conditions in the oil palm crop agricultural research center in Pobè in southern Benin (7° North and 2°40' East), which occupies approximately 700 ha and has an annual rainfall 1,200 mm. In addition to agronomy trials, the plantations are composed of a wide variety of breeding populations in a collection used for the production of improved oil palm seeds.

The observations focused on 10 breeding populations of oil palms aged 8 yr and over: four *E. guineensis* populations (originating from La Mé and Yocoboué in Ivory Coast, Yangambi in the Democratic Republic of Congo and Deli in Indonesia) ([Corley and Tinker 2003](#)), two *E. oleifera* populations (originating from Brazil and Central America), and four backcrosses ($Eg \times Eo$) \times Eg (PO 6222, PO 6322, PO 6271, PO 5238) ([Le Guen et al. 1991](#)). The scarcity of $Eg \times Eo$ F1 hybrid palms at the station prevented us from including that type of material in the observed palms. The numbers of palms observed for each breeding population are listed in [Table 1](#).

The study of *C. lameensis* oviposition and survival on different breeding populations under no-choice conditions was carried out experimentally using the sleeve technique described by [Morin and Mariau \(1971\)](#), [Philippe \(1977\)](#), [Coffi \(2006\)](#), and [Coffi et al. \(2009\)](#). A large sleeve was installed around a healthy and accessible rank 17 frond that contained approximately 120 healthy leaflets. The sleeve was made of a very fine mesh (100 μ m in diameter) muslin type fabric, pulled taut by two metal hoops (6 mm in diameter) linked together by a plywood lath (0.5-mm thick). Each sleeve measured 2.5 m in length by 1.10 m in diameter.

C. lameensis imagos of unknown age were collected from some infested palms at the Pobè station. One hundred fifty individuals (50 males and 100 females) were placed in each sleeve. After 3 d, during which the individuals mated and laid eggs, they were all removed from the sleeve. The sleeves were left on each palm for the complete *C. lameensis* life cycle, i.e., 12 wk. The number of living and dead eggs, and first- and second-instar larvae was counted by sampling a third of the leaflets after 4 wk at a rate of every third leaflet. The number of living and dead eggs, and all-instar larvae was counted by sampling

Table 1. Number of palms sampled for no-choice sleeve tests and physical characteristics of leaflet measurements

Species	Breeding populations	No-choice sleeve tests	Physical characteristics of leaflets
<i>E. guineensis</i>	La Mé	4	4
	Yocoboué	0	4
	Yangambi	4	4
	Deli	4	4
<i>E. oleifera</i>	Brazil	2	4
	Central America	2	4
Back crosses	PO 6222	3	4
	PO 6322	4	13
	PO 6271	2	5
	PO 5238	3	9

the second third of the leaflets in the 8th wk at a rate of every other leaflet. Lastly, the remaining leaflets sampled in the 12th wk were used to count the number of living and dead all-instar larvae, pupae, and imagos.

In all, three series of sleeve installations were carried out on each of the 28 palms in June 2009, September 2009, and February 2010.

For the epidermis and cuticle measurements, a leaflet was taken from each palm at point B of the rank 17 frond (Jacquemard, 1995). A sample of 10 cm from the middle of each leaflet was isolated. The measurements were taken on six cross-sections spread regularly along the 10 cm of the sample. The cross-sections were made with a razor blade perpendicular to the midrib of the leaflet sandwiched in cassava or millet pith. The cross-sections were soaked in bleach for 15 min. Once rinsed, they were transferred to Mirande's reagent for 5 min to stain the cells of the epidermis and the cuticle pink, followed by final rinsing. The epidermis and cuticle thickness measurements were carried out under a microscope (Leica DM 2500P) fitted with an ocular micrometer with respective enlargements of $\times 10$ and $\times 40$. The histological sections were made and observed at the Plant Biology Laboratory of the science and techniques faculty of the University of Abomey-Calavi in Benin.

The thickness of the cuticle and the thickness of the epidermis were calculated for each palm individual, taking the average of the six measurements.

Data Analysis. Insects survival and their development dynamics on the different breeding populations was assessed by the observed fertility of the introduced adults and the percentages of transition from one stage to the next for their offspring. The effect of the studied factors and experimental conditions on these development dynamic parameters was tested by applying a Generalized Linear Mixed Model (PROC GLIMMIX, SAS Institute 2011) with an appropriate probability distribution for each parameter and with its canonical link function. The goodness of fit of the model formed by the distribution and the introduced fixed and random effects was assessed by the ratio of the chi-square statistics and its degrees of freedom.

Variations in the number of eggs laid depending on the series, the breeding population, and the number of weeks after mating were analyzed with a negative binomial distribution, as suggested by a preliminary checked nonlinear mean-variance relationship. The model included breeding population \times number of weeks interaction and took into account random effects corresponding to each sampling round (i.e., a given number of weeks in a series of observations), each palm tree, and each sleeve. The χ^2 by df ratio was equal to 1.00.

Variations in the rate of transition from one stage to the next depending on the series, the breeding population, and the number of weeks were studied with a Binomial distribution. The model included the main effects and took into account random effects corresponding to each palm tree, each sleeve, and each specific sample took in one sleeve. The mean hatching percentages were computed for the three numbers of weeks, whereas the other transition rates were computed only after 8 and 12 wk. The χ^2 by df ratio varied between 0.5 and 0.8 according to the transition studied.

The differences in cuticle and epidermis thickness between breeding populations were analyzed by an analysis of variance followed by a Turkey–Kramer test.

The correlation between the insect development parameters and the physical characteristics of each breeding population was assessed graphically and by calculating Pearson's coefficient of correlation.

Results

Study of Oviposition and Survival of the Different *C. lameensis* Instars Under No-Choice Conditions. The analysis of variations in the total number of eggs laid depending on the series, the breeding population, and the sampling weeks is reported Table 2. It revealed major differences in oviposition between the series of observations; for all breeding populations combined, an average of 22 (95% confidence interval [CI]: 15–35) insects per sample were found in the first two series, as opposed to only 9 (95% CI: 6–13) individuals per sample found in the third series. The estimations of the number of eggs laid decreased from 21 (95% CI: 17.1–27.6) for the 4-wk sampling to 12 (95% CI: 9.5–14.2) for the 12-wk sampling. This artifact may come from difficulties to identify dead eggs and larvae after a few weeks. With respect to the different breeding populations, the average number of eggs laid was between 9.8 eggs per sample (observed for the Yangambi origin) and 27.3 eggs per sample (observed for the La Mé origin) (Table 3). Only the difference between these extreme values was significant ($P < 0.05$ using the Tukey's test). There was no significant difference between the two *E. oleifera* breeding populations, the *E. guineensis* Deli origin, and the PO 6271, PO 6322, PO 6222, and PO 5238 backcrosses (Fig. 1).

The analysis of variations in the rate of transition from one stage to the next depending on the series, the breeding population, and the sampling week is reported in Tables 4 and 5. It showed that the average hatching percentage was significantly higher on the La Mé origin (80%) than on the Deli origin (28%). The hatching percentage for the other origins had intermediate values that were not significantly different from the extreme values. In particular, no significant difference was found between the average hatching percentage for the *E. oleifera* (45 and 48%) and the *E. guineensis* breeding populations (Fig. 2).

For the transition of first- and second-instar larvae to the third- and fourth-instar larvae, the results calculated for the last two sampling operations showed a highly significant difference in the average percentage of individuals passing to third- and fourth-instar larvae between the La Mé origin and the PO 6271 backcross on the one hand (87% and 79%) and the two *E. oleifera* breeding populations on the other hand (0% for the South America origin and 2.8% for the Brazil origin). The Deli and Yangambi origins and the PO 6222, PO 6322, and PO 5238 backcrosses had intermediate average rates (11–59%, Fig. 3).

Lastly, for the transition of the third- and fourth-instar larvae to pupae, the average rate of individuals having shed could not be estimated properly for the two *E. oleifera* breeding populations because the

Table 2. Type 3 tests for GLMM analysis of number of eggs laid

Effect	df	F	ProbF
Series	2 62	18.8	<0.0001
Number of weeks	2 130	12.2	<0.0001
Breeding population	8 21	2.8	0.0282
No. of weeks \times breeding population	16 135	2.9	0.0004

GLMM, generalized linear mixed model.

Table 3. Type 3 tests for GLMM analysis of rate of transition

Effect	Hatching				1&2 IL \rightarrow 3&4 IL transition				3&4 IL \rightarrow pupa transition			
	df	F	ProbF		df	F	ProbF		df	F	ProbF	
Series	2	55	0.8	0.4510	2	29	1.8	0.1769	2	6	1.2	0.3535
Number of weeks	2	118	0.1	0.9337	1	31	0.9	0.3560	1	6	4.3	0.0836
Breeding population	8	20	2.9	0.0238	7	16	4.8	0.0047	4	5	0.6	0.6654

GLMM, generalized linear mixed model.

number of individuals reaching the third- and fourth-larval instars was too small. There was no significant difference between the other breeding populations (Fig. 4).

The fate of the insects after the pupal stage (metamorphosis into imago or dead) could only be certified on very few individuals, even after 12 wk (third sampling). Under these conditions, it was not possible to perform the analysis of variations for the rate of transition from the pupal stage to the adult stage.

These results take into account the absence of parasitoids and predators under our experimental conditions.

Comparison of the Epidermis and Cuticle for Different *Elaeis* spp. Origins. The analysis of variance revealed highly significant differences of epidermis thickness between the two species ($F=59.6$;

$df=2,45$; $P<0.001$). *E. oleifera* had a significantly thicker epidermis than *E. guineensis* ($17\text{ }\mu\text{m}$ [SE = 0.5] on average, as opposed to $12\text{ }\mu\text{m}$ [SE = 0.3] on average) and the five backcrosses ($11\text{ }\mu\text{m}$ [SE = 0.3] on average, Fig. 5).

The differences between the breeding populations within the species are also significant ($F=3.3$; $df=7,45$; $P<0.01$). There was no difference between the Brazil and Central America origins of *E. oleifera* for which the epidermis thickness was $17\text{ }\mu\text{m}$ (SE = 0.7) on average (Fig. 6). The Yocoboué origin had a slightly thinner epidermis than the other three *E. guineensis* breeding populations, Deli, Yangambi, and La Mé, between which there was no significant difference.

The cuticle thickness appeared significantly different between species ($F=13$; $df=2,45$; $P<0.001$). The *E. oleifera* had a significantly thicker cuticle ($4\text{ }\mu\text{m}$ [SE = 0.1] on average) than the *E. guineensis* species, which had a cuticle of $2\text{ }\mu\text{m}$ (SE = 0.1) on average. The cuticle of the backcrosses had an intermediate thickness ($3\text{ }\mu\text{m}$ [SE = 0.1], Fig. 7).

Within the species, significant differences exist ($F=11,7$; $df=7,45$; $P<0.001$). No difference was found in cuticle thickness between the two *E. oleifera* ($4\text{ }\mu\text{m}$ [SE = 0.2] on average), but two significantly different groups were found in the *E. guineensis* species: Deli and Yangambi ($2.5\text{ }\mu\text{m}$, SE = 0.2) and La Mé and Yocoboué ($1.2\text{ }\mu\text{m}$, SE = 0.2), which had a thinner cuticle on average (Fig. 8).

The graphs (Figs. 9 and 10) illustrate the conjunction found between the survival of *C. lameensis* first- and second-instar larvae and the epidermis and cuticle thicknesses of the different breeding populations studied. The coefficient of correlation amounted to -0.6 for epidermis thickness and -0.8 for the cuticle, which seemed mainly due to the opposition between the *E. guineensis* La Mé origin and the *E. oleifera*.

Table 4. Mean number of eggs laid for the breeding populations

Breeding population	Mean	Standard error	Lower 95% CL	Upper 95% CL
LAME	27.3	4.9	18.7	39.7
YANG	9.9	1.9	6.6	14.8
DELI	20.6	3.9	13.9	30.6
OLAM	17.4	4.7	9.9	30.4
OLBR	11.1	3.0	6.3	19.6
PO6222	12.8	2.8	8.1	20.2
PO6322	21.1	4.0	14.2	31.3
PO6271	21.7	5.8	12.4	37.9
PO5238	14.6	3.2	9.3	23.1

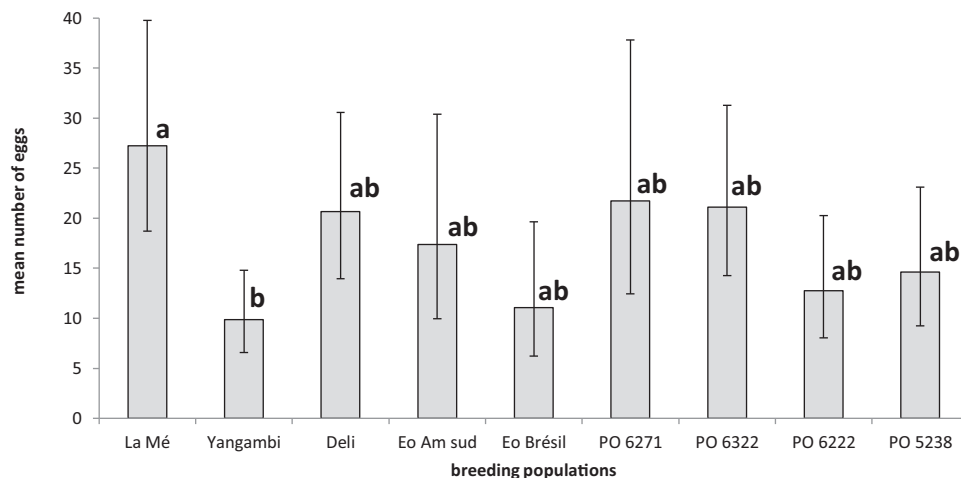


Fig. 1. Mean number of eggs laid by *C. lameensis* for different breeding populations. Means with the same letter are not found significantly different by the negative binomial GLMM followed by Tukey's HSD test ($P<0.05$). Bars give 95% confidence limits. GLMM, generalized linear mixed model.

Table 5. Mean transition rate for the breeding populations

Breeding populations	Hatching percentages				1&2 → 3&4 IL transition percentages				3&4 IL → pupa transition percentages			
	Mean (%)	Standard error	Lower 95% CL	Upper 95% CL	Mean (%)	Standard error	Lower 95% CL	Upper 95% CL	Mean (%)	Standard error	Lower 95% CL	Upper 95% CL
LAME	79.7	6.9	61.9	90.5	86.9	7.7	61.3	96.5	95.5	6.3	32.7	99.9
YANG	42.4	11.9	21.0	67.1	36.9	25.8	5.3	86.0	75.9	56.7	0.1	100.0
DELI	27.7	8.5	13.6	48.2	17.0	10.9	3.9	51.1	95.5	10.4	3.8	100.0
OLAM	48.4	14.7	21.5	76.2	0.0							
OLBR	44.6	14.9	18.6	73.9	2.8	3.0	0.3	23.0	0.0			
PO6271	73.9	11.4	45.3	90.6	78.7	14.1	38.4	95.6	95.9	8.0	11.8	100.0
PO6322	34.4	9.8	17.4	56.5	10.8	8.2	1.9	42.3	0.0			
PO6222	36.7	12.5	15.9	64.1	59.1	31.2	8.5	95.7	25.7	45.8	0.1	99.4
PO5238	34.8	11.2	16.0	59.8	13.8	10.4	2.4	50.4	0.0			

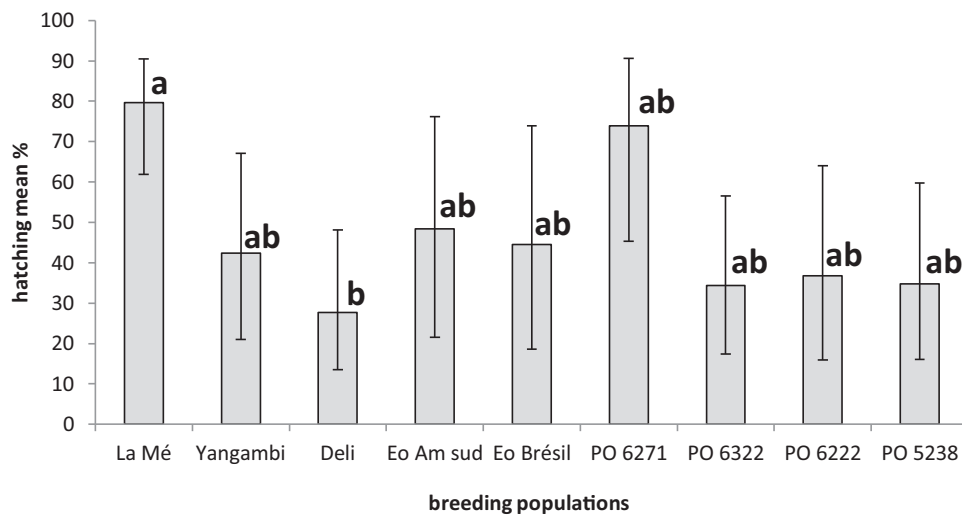


Fig. 2. Mean hatching rate for different breeding populations. Means with the same letter are not found significantly different by the binomial GLMM followed by Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits. GLMM, generalized linear mixed model.

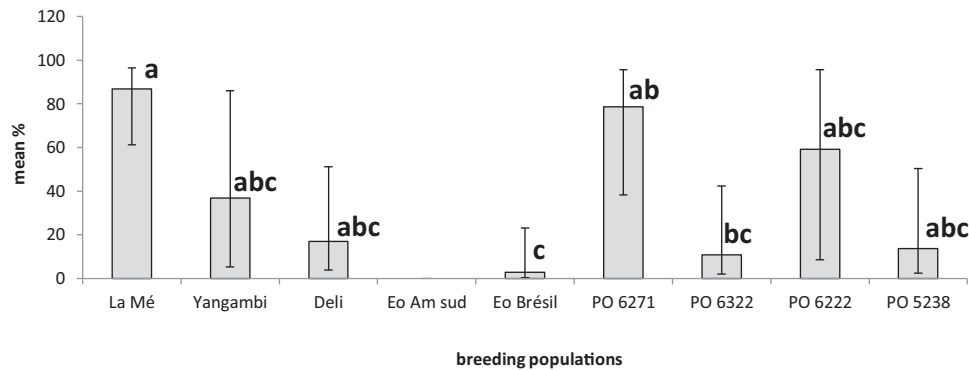


Fig. 3. Mean rate of transition from first- and second-larval instars to third- and fourth-larval instars for different breeding populations. Means with the same letter are not found significantly different by the binomial GLMM followed by Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits. GLMM, generalized linear mixed model.

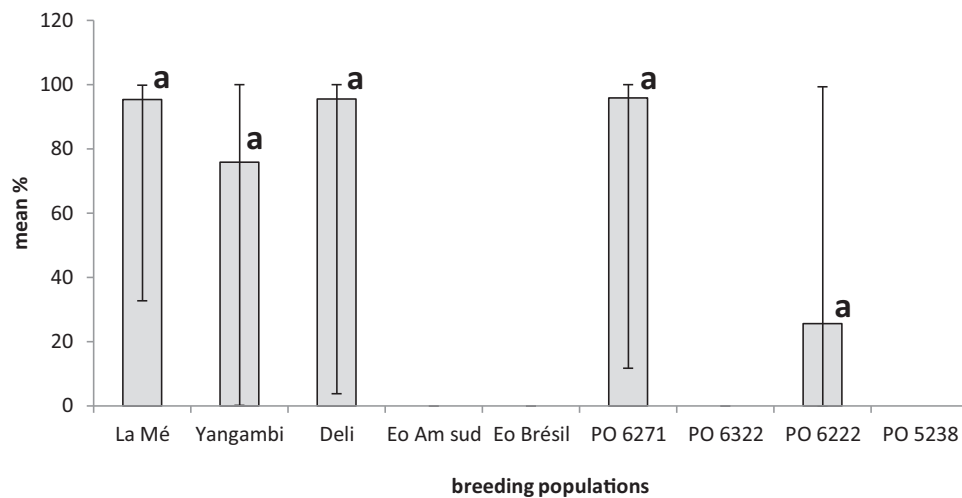


Fig. 4. Mean rate of transition from third- and fourth-larval instars to pupa stage for different breeding populations. Means with the same letter are not found significantly different by the binomial GLMM followed by Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits. GLMM, generalized linear mixed model.

Discussion

The results showed that the genetic variability of the different oil palm breeding populations played a very important role in the survival rate of *C. lameensis*. In addition, the thickness of the epidermis and the cuticle indicated the edibility of the different breeding populations and whether the breeding populations were suitable for the survival of *C. lameensis*. *E. oleifera*, with a thick cuticle (4 μm) and epidermis (17 μm), proved less conducive to *C. lameensis* development than *E. guineensis*, which had a thinner cuticle (2 μm) and epidermis (12 μm).

This result agreed with the fact that *E. oleifera* is more resistant than *E. guineensis* to *C. lameensis* attacks. The properties of these two species were confirmed by earlier observations by Philippe (2003, 2006) and by results obtained under natural conditions (Coffi et al. 2013). However, our study is unique because we used breeding populations well defined that are representative of what is likely to be used in an actual oil palm breeding scheme. Additionally, the use of no-choice conditions allows the individual assessment of breeding populations. Quantitative counting allowed the identification of the stages during which resistance occurs; until now, only qualitative observations of foliage damage have been available. Ours is the first attempt to link resistance to the physical parameters of the fronds.



Fig. 5. Comparison of the mean epiderm thickness for *E. oleifera*, *E. guineensis*, and the backcrosses. Means with the same letter are not found significantly different by the Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits.

The results from the sleeve studies showed that *C. lameensis* mated and then deposited their eggs similarly on the different breeding populations tested. The foliage was therefore not a limiting factor for oviposition. This result suggested that the females did not discriminate between oil palm breeding populations in an olfactory or visual manner. Even *E. oleifera*, which appeared less suited to larval development, did not display any repellent effect for female oviposition. It is therefore not very likely that mechanical properties affect oviposition. A comparative study was undertaken on the leaf beetle *Disonycha pluriligata*. It showed that females did not have an oviposition preference (Marques et al. 1994). Indeed, oviposition preference is assumed to be largely correlated to the survival of the progeny. For instance, a tree chosen by a pine sawfly female to deposit its eggs may not be suitable for the survival of larvae (Pasquier-Barre et al. 2000). Several studies reveal that oviposition preference is not simply correlated to the successful development of the progeny (Bernardo 1996) but rather to environmental factors such as predation (Björkman et al. 1997), earlier pest attacks (Leather et al. 1987, Hilker and Weitzel 1991), abiotic stress (Tisdale and Wagner 1991, Saikkonen et al. 1995), and the chemical characteristics of the foliage (Leather et al. 1987, Olofsson 1989). Adaptation of the insect is maximized if oviposition takes place on a plant suited to the development of eggs and larvae (Thompson and Pellmyr 1991,

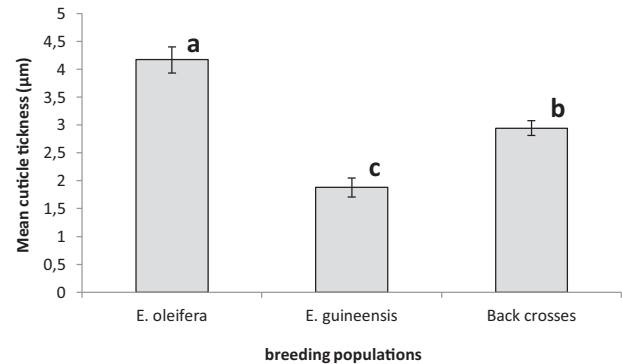


Fig. 7. Comparison of the mean cuticle thickness for *E. oleifera*, *E. guineensis*, and the backcrosses. Means with the same letter are not found significantly different by the Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits.

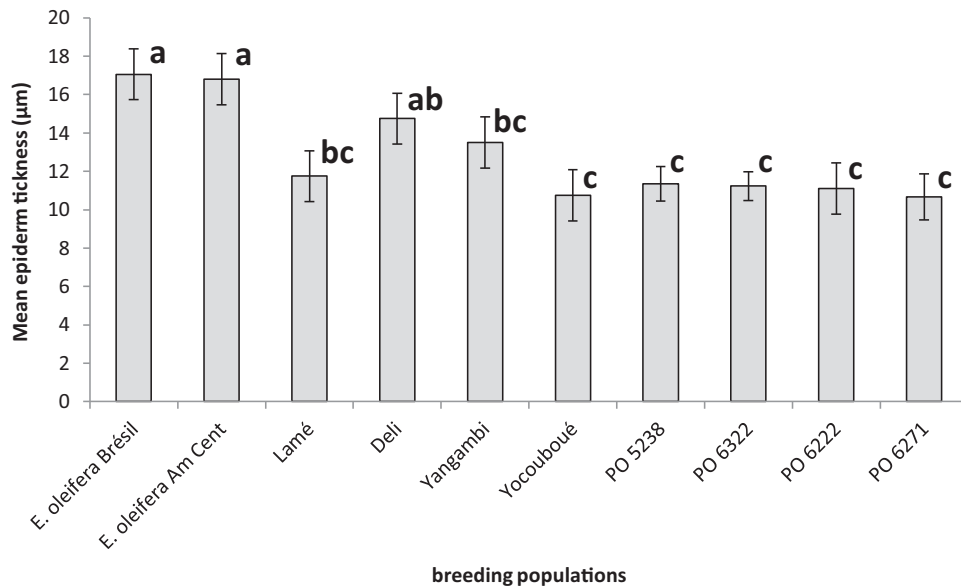


Fig. 6. Mean epiderm thickness for different breeding populations. Means with the same letter are not found significantly different by the Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits.

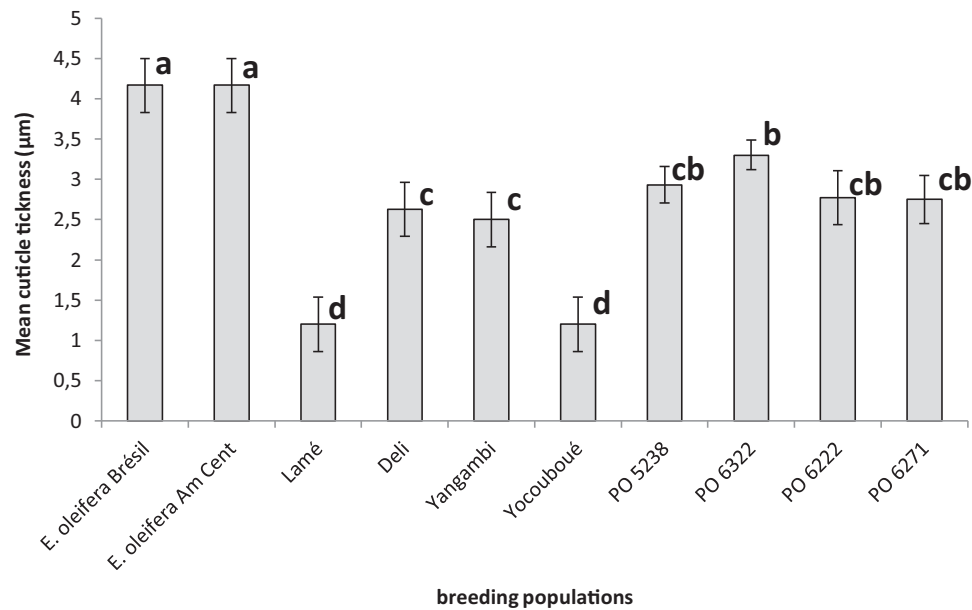


Fig. 8. Mean cuticle thickness for different breeding populations. Means with the same letter are not found significantly different by the Tukey's HSD test ($P < 0.05$). Bars give 95% confidence limits.

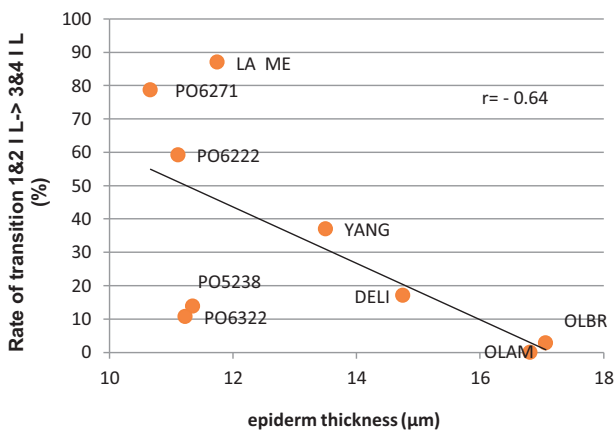


Fig. 9. Correlation between mean epiderm thickness and rate of transition between larval instars for different breeding populations.

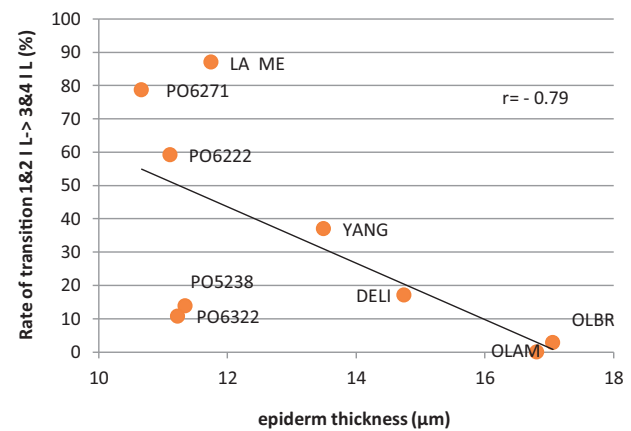


Fig. 10. Correlation between mean cuticle thickness and rate of transition between larval instars for different breeding populations.

Tisdale and Wagner 1991). Few studies have sought to determine the role of the genetics of the plant in this process (Bingaman and Hart 1992, Craig 1999).

It was only after hatching that consumption slowed down on the unsuitable breeding populations. The average rate of transition of first- and second-instar larvae to third- and fourth-instar larvae was 0 for the *E. oleifera* from South America and under 2% for the *E. oleifera* from Brazil. The average percentage of larvae passing from first and second to third and fourth larval instars can reach 87% for the La Mé origin, as shown by the observations of Philippe (2006), where this origin was more severely attacked than the Deli, Yangambi, and backcrosses. At this particular period of the insect's cycle, the breeding population seemed to have a substantial influence on the insect's development. This was confirmed for the third- and fourth instars—pupa transition for the *E. oleifera* population originating from Brazil, on which its development was not continued. Mortality linked to the breeding population was mentioned by Mariau (2001), who found an average larval mortality of 70% on *E. guineensis* and 97.2% with the interspecific hybrid. Although it is known that the insect stops feeding during the pupae stage, this stage proved to be critical for insects deposited on palms of the Yangambi origins and palms of the PO 6322 and PO 5238

backcrosses. These breeding populations seemed to affect the final development of the insects, which did not reach the adult stage. The analysis of the rates of transition of first- and second-instar larvae to third- and fourth-instar larvae was based on relatively high numbers at the outset (around a dozen larvae) and appeared more reliable than analyzing the rate of passage of third- and fourth-instar larvae to pupa, for which the numbers involved were too small. The results obtained at the end of our research showed that *E. oleifera* did not ensure the development of *C. lameensis* from egg to imago. With respect to the PO 6322 and PO 5238 backcrosses, the average behavior observed in the four individuals of the sample showed that these palms displayed character traits specific to their *E. oleifera* ancestor. However, the small number of individuals did not enable us to reach any conclusion regarding the backcrosses or regarding the mechanism by which the resistance traits were genetically transmitted. A. C. (personal communication) found that these facts were quite similar to some observations showing that the consumption of leaflets on young nursery palms or palms that have not started bearing did not sustain the development of *C. lameensis* populations.

The relationship between the cuticle–epidermis morphological criterion and the ability of the breeding population to ensure the

development of the insects was clearly shown. It revealed that the mechanical properties of the foliage were able to limit feeding, which led to developmental problems and larval mortality. Our results confirmed some earlier histological observations that showed that the thicker the epidermis of the palms was, the less the oil palm plantations were infested by the pest (Coffi 2006, Philippe 2006). Although the thickness of the cuticle and epidermis can affect the edibility of the foliage for the insect (Tanton 1962, Raupp 1985, Ohmart et al. 1987), larval mortality might have resulted from other factors linked to the host plant, such as the existence of certain compounds (Feeny et al. 1997). For example, cumulative toxicity or insufficient nutrient uptake may cause a deficiency in growth factors or a lack of energy reserves to ensure molt. The higher mortality found for the first- and second-instar larvae and, to a lesser degree, the third- and fourth-instar larvae might be explained by the consumption of a lethal dose of some plant active substances. In fact, the accumulation of the said substances inside the pest over time, from the least advanced stages (egg, first-instar larvae) to the most advanced stages (starting from the second-instar larvae), would seem to have enabled the lethal dose to be reached, causing the death of more than 50% of *C. lameensis*. If adults do not effectively perceive any differences in the plants at the time of oviposition, the hypothesis of cumulative intoxication of larvae caused by different chemical compounds not perceptible to imagoes can be proposed. Under laboratory conditions, Coffi et al. (2012) showed that leaflet extracts from *E. oleifera* were toxic to *C. lameensis*. It is also possible that antibiosis-type defense mechanisms may exist in oil palms (Painter 1951). Under natural conditions, such larval mortality could be even higher, as the action of parasites and predators would be added to the unfavorable influence of the host plant factors.

Substantial *Coelaenomenodera* egg mortality has been observed on the interspecific hybrid (39% as opposed to 26.1% on *E. guineensis*), with a clear difference for young larvae (89.1% mortality as opposed to 46.6%) (Philippe 1977). Some other researchers have shown a correlation between feeding and oviposition preferences for two species of leaf beetles for 15 poplar clones (Augustin et al. 1993). Likewise, Auger et al. (1990, 1992) identified some clones that were suited or unsuited to the survival of *Diprion pini*, a pest on Scots pine.

Conversely, several oil palm progenies compared in Ghana did not reveal any significant difference for the development duration of the different *C. lameensis* stadia (Appiah et al. 2007, Dinkpa et al. 2010). The results did not show whether the breeding population affected the insect's cycle in a qualitative manner, i.e., whether the edibility of the foliage might play a role in the feeding of larvae, hence their development. Consequently, this suggests that the edibility of the foliage of the different breeding populations might be linked to their chemical composition. However, the literature does not provide any indication of the variations in the biological performance of insects related to their feeding: mortality, duration of larval development, insect weight, or fecundity. Lastly, our results revealed that the larvae hatched from the first eggs laid on the least susceptible material were able to cause substantial damage to the palms until the end of larval development, but as there were no progeny, the populations were not renewed; thus, the extent of the damage was limited. On the other hand, on the susceptible material, the insect completed its cycle, thereby ensuring renewal of the pest generations and maintaining a population level causing economically harmful damage.

From a methodological viewpoint, in the absence of the possibility of early testing on young nursery palms, biological tests in sleeves remain the only reliable method for determining the ability of oil palms to sustain the development of the pest. A. C. (personal communication) confirmed that the foliage of young nursery palms was not consumed and that *C. lameensis* showed a preference for old palms (Cotterell 1925). These observations suggest that the "breeding population" and "foliage age" factors might act in different ways, involving different chemical compounds and mechanical properties, though they have a similar effect on a large number of the insect's developmental characteristics.

The methods developed using sleeves for biological tests are reliable; however, as stated in the Results section, there appeared to be some large differences between the series of observations for the observed oviposition rates of transition from one stage to the next. This lack of repeatability shows the major effect of climatic factors and other environmental conditions on the results of such tests.

In addition, even for the breeding populations suited to *C. lameensis* development, few eggs were laid. Yet, the reproductive capacity is particularly high (Mariau et al. 1981, Mariau 2001). It was also noted that the mortality percentages were calculated on few individuals for the last two transitions: third- and fourth-instar larva—pupa and pupa-imago.

The drawback of tests in sleeves could be excessive heat that might lead to the desiccation of young larvae (Cotterell 1925, Mariau and Morin 1974). Although the parasitoid parameter can be discarded, the survival of eggs and larvae can vary depending on the temperature (Morin and Mariau 1974). Cachan (1957b) found that some *Coelaenomenodera* outbreaks in Benin and Ivory Coast followed an abnormal drop in temperatures over several generations. Conversely, the severe dry seasons in Benin led to a notable reduction in the pest (Morin and Mariau 1974). Mortality at the egg stage depends less on parasitism than on climatic factors (Mariau 2001). The conditions for maintaining adults and the different larval instars in sleeves play a part in disrupting the microclimate and the survival conditions of the individuals. It was shown by Mariau and Lecoustre (2000) that the different climate components, especially a deficit in the saturation of the air, play a major role in egg mortality. It increases with the temperature and dryness of the air. A humid atmosphere leads to an increase in fecundity and a drop in egg mortality (Mariau 2001). These considerations suggest some possible improvements to the in situ test protocol, such as multiplying the number of replications under varied atmospheric conditions and adopting the muslin of the sleeves that induce minimal environmental disruptions.

Based on the observations and results of this experiment, it can be said that *E. oleifera* material is more resistant, while the La Mé, Deli, and Yangambi materials are the most susceptible, in decreasing order, to attacks by the pest because they enable the insect to complete its life cycle and thereby give rise to a new generation. For the PO 6271 and PO 6222 backcrosses, the average susceptibility proved to be intermediate between the two species but probably contained variability in susceptibility between palms that the protocol was unable to detect on an individual level.

Conclusion

The way in which the oil palm breeding population affects *C. lameensis* is of great interest and offers some interesting prospects for breeding resistant palms or palms with low vulnerability.

The discovery of a correlation between the characteristics of the epidermis and larval survival on different breeding populations is a first step in the search for resistant oil palm breeding populations and in identifying some potential resistance mechanisms. The work presented here provides some new information on the interactions between *C. lameensis* and *Elaeis* sp. with different breeding populations and the varied abilities of the latter to sustain the insect's development.

The discovery that *E. oleifera* is not suited to the development of *C. lameensis* justifies the program to introgress its resistance in *E. guineensis* via backcrosses.

Our results showed that a more in-depth study will have to be undertaken to determine the precise nature of the toxicity of the foliage of the *E. oleifera* species.

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